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ARE HIGH DENSITIES OF FISHES AT ARTIFICIAL REEFS THE RESULT OF HABITAT LIMITATION OR BEHAVIORAL PREFERENCE?

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ABSTRACT

Rapid colonization, high fish densities, and high catch rates at artificial reefs have been used as evidence for habitat-limitation and increased production of reef fishes. An alternative hypothesis is that artificial reefs attract fishes due to behavioral preferences but do not increase reef fish production or abundance. Reviewed literature reveals that except in one case evidence for increased production is mostly anecdotal and inadequate. Attraction and/or production by a particular artificial reef is predicted to depend on the species and individual ages (size) of reef fish, and on reef location. Factors predicted to be important are natural reef availability, mechanisms of natural population limitation, fishery exploitation pressure, life history dependency on reefs, and species-specific and age-specific behavioral characteristics. Increased production is most likely at locations isolated from natural reefs, and for habitat-limited, demersal, philopatric, territorial, and obligatory reef species. Attraction should be more important in locations with abundant natural reef habitat; where exploitation rates are high; and for recruitment-limited, pelagic, highly mobile, partially reef-dependent, and opportunistic reef species. Artificial reefs are unlikely to benefit heavily exploited or overfished populations without other management actions.

Artificial reefs are used in fisheries to create fishing opportunities, reduce user conflicts, save time and fuel, reduce fishing effort, make locating fish more predictable, increase public access and safety by deployment near ports, and increase fish abundance at deployment sites by attracting dispersed fishes and producing new fish biomass (Stone, 1985; National Academy Press, 1988).

Questions persist, however, about the importance of artificial reefs for producing new fish biomass versus attracting and aggregating fishes from surrounding areas without increasing total biomass (Bohnsack and Sutherland, 1985; Munro and Williams, 1985; Solonsky, 1985; Bohnsack, 1987; National Academy Press, 1988). The resolution of this controversy has important implications for fisheries management. Artificial reefs that produce significant new biomass may be useful for increasing fishery resources. However, artificial reefs that act primarily by attraction may promote overfishing under heavy fishing pressure by increasing fish catchability (the proportion of the population removed by one unit of effort). Fishes normally dispersed over a wide area would be concentrated and possibly depleted more rapidly (Samples and Sproul, 1985).

An underlying rationale for artificial reef deployment is the production hypothesis: that artificial reefs provide additional critical habitat that increases the environmental carrying capacity and eventually the abundance and biomass of reef fishes. Barren, unproductive substrate is turned into a highly productive environment (Stone et al., 1979). Mechanisms suggested for this transformation include (1) providing additional food, (2) increasing feeding efficiency, (3) providing shelter from predation, (4) providing recruitment habitat for settling individuals that would otherwise have been lost to the population, and (5) indirectly, because fishes moving to artificial reefs create vacated space in the natural environment that allows replacement from outside the system (Randall, 1963; Ogawa, 1973; Stone et al., 1979; Matthews, 1985).

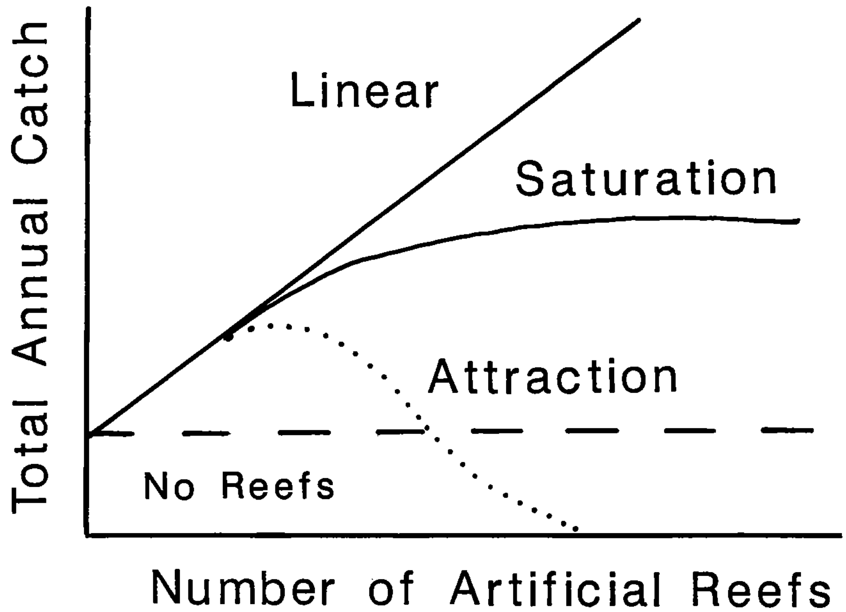

Figure 1. Predicted effects of the attraction and production hypotheses on catch. The production hypothesis predicts increased catch as some function of the amount of deployed reef material (solid lines). The attraction hypothesis (dotted line) predicts an initial increase in catch followed by stock depletion and decline to levels below ambient catch without artificial reefs (dashed line). See text for details.

An alternative attraction hypothesis is that artificial reefs attract fishes as the result of behavioral preferences but do not significantly increase total fish biomass.

Possible effects of the production and attraction hypotheses on catch are illustrated (Fig. 1). The production hypothesis predicts that biomass production and catch will increase as some function of the amount of material deployed. Possibilities include direct linear or saturation functions. Saturation results when reef resources no longer limit populations so that constructing additional reefs does not further increase production. The attraction hypothesis predicts as a worst case an initial increase in catch followed by a decline to levels below what existed without artificial reefs. Total catch should eventually fall because of depletion due to increased catchability. However, higher total catch may be sustained under the attraction hypothesis if replacement occurs from a large stock of migratory individuals (not illustrated).

A better understanding of the relative importance of attraction and production is critical for wise fisheries management and the effective construction and deployment of artificial reefs. Although the controversy has been recognized for a long time, progress toward resolving it has been slow. Here I attempt to elucidate the controversy and facilitate its resolution by recasting it into a theoretical and testable framework.

Methods

I reviewed the relevant scientific literature emphasizing reef fish ecology, population limitation, behavior, and effects of artificial reefs on fish populations. Some described behavioral attraction mechanisms have not been tested on fishes although examples using fish were cited where possible. Based on the review I predicted conditions under which attraction (reefs primarily aggregate fishes without necessarily increasing biomass) or production (reefs increase biomass by providing shelter or food for resource-limited populations) should operate. Existing data and experimental approaches for testing the relative importance of attraction and production are discussed.

Reefs were broadly defined to include true coral reefs, rock outcroppings, wrecks, fish aggregating devices (FADs), oil production platforms, breakwaters, and other artificial structures. For this paper reef fishes include any fish frequently associated with natural or artificial reefs. Recruitment was defined as the process of larval settlement and post-settlement survivorship to initial census observation (Richards and Lindeman, 1987). Production was defined as the net increase in fish biomass, not harvest rate or harvest quantity (Bohnsack and Sutherland, 1985). Growth overfishing was defined as the process of harvesting fishes before they have had a chance to put on weight; recruitment overfishing was defined as the process of reducing adult stocks to a point where recruitment fails from a lack of sufficient larvae (Cushing, 1973).

RESULTS

Reef Fish Ecology

Life History.—Reef fish biology and fisheries have been reviewed by Sale (1980), Huntsman et al. (1982), Munro (1983), Polovina and Ralston (1987), and Richards and Lindeman (1987). Almost all reef fishes have a planktonic larval dispersal phase that lasts from weeks to months (Sale, 1980; Brothers et al., 1983; Victor, 1986b). Many reef fishes are sedentary; after their young settle directly on reefs, they remain there for the rest of their lives. Many commercially and recreationally important reef fishes such as lutjanids, serranids, haemulids and sphyraenids settle in other habitats before moving to a reef (Starck, 1968; 1970; Moe, 1969; Shulman and Ogden, 1987). Obligate reef species require reef habitat while opportunistic species may use reefs as well as other habitats. Some species move off a reef daily to feed in surrounding areas (reviewed by Helfman, 1986). Many commercially and recreationally important reef fishes are characterized by long life, slow growth, low natural mortality, and high reef fidelity (Huntsman, 1981; Manooch, 1987). Factors generally considered most likely to limit adult population size are habitat, larval supply (recruitment), and fishery exploitation (Sale, 1980; Richards and Lindeman, 1987).

Habitat Limitation.—The belief that animal populations exist close to the carrying capacity of an environment is well established in ecological literature (MacArthur, 1972), especially for more stable environments (Menge and Sutherland, 1976). Reef fish abundance has traditionally been considered limited by habitat or space partly because reefs are a patchy resource, limited in geographical coverage and separated from other reefs. Sale (1980) noted a widespread assumption that the number of larvae able to settle on natural reefs was in excess of the resources available after settlement. Competitive interactions among individuals was thought to determine abundance on a reef (Sale, 1980; Munro and Williams, 1985), and scarcity of reefs limited sustained fishery yields (Huntsman, 1981).

Habitat is thought to be limiting primarily by availability of food or shelter from predation. Shelter is generally considered more important (Sale, 1980) although proximity of food in sea grasses and plankton availability may limit some fish populations (Randall, 1963; Glynn, 1973). Shulman (1984) found that food availability did not directly influence settlement or early survivorship. Ross (1986) suggested, however, that food limitation was more important than generally recognized based on evidence that trophic resource partitioning was more important than habitat partitioning among temperate and possibly tropical marine reef fish assemblages. Richards and Lindeman (1987) noted that food shortage can be difficult to show because starvation and slower growth interact with predation.

Predation has been shown to be an important source of mortality especially among newly settled juveniles (Shulman, 1984; Doherty and Sale, 1986; Shulman and Ogden, 1987). Shulman (1984) found shelter site availability limited recruitment and/or early survivorship presumably through its effects on predation rates. Hixon and Beets (1989) showed inverse relationships between prey and predator abundance influenced by shelter availability.

Sale (1980) concluded that space-limited assemblages existed but were less general than previously claimed. Out of four studies claiming a relationship between species richness and topographic complexity, only two (Risk, 1972; Luckhurst and Luckhurst, 1978) demonstrated such a relationship (primarily for sedentary species). Sale (1980) noted that four lines of evidence were used to support the importance of topographically structured space-limitation for reef fishes: (1) the very rapid colonization of artificial reefs and denuded natural reefs; (2) faster recruitment to empty versus occupied natural and artificial reefs; (3) conspicuous interspecific territorial defenses; and (4) constancy of numbers in some sites and microhabitats. Sale rejected the constancy of numbers as evidence after noting many reports of wide variations of fish abundance, even by authors concluding persistence of fish assemblages. Bohnsack (1983) showed that the appearance of constancy could be an artifact of the time interval between censuses.

Sale (1980) concluded that competitive and predatory responses by resident fishes did not always influence recruitment rates. Munro and Williams (1985) concluded that with the exceptions of Sale (1976) and Shulman et al. (1984), most studies found either no recruitment inhibition or enhanced recruitment by resident populations. Shulman (1985b) concluded that spatial patterns of recruitment interacting with predation may influence population abundances and species composition of reef fishes. Sweatman (1985) found high resident fish densities reduced larval recruitment by other fish species but this response was not related to resource availability. Jones (1987) found for one damselfish that juvenile density or adult presence had substantial effects on growth and maturation but not on juvenile survivorship.

Recruitment Limitation.—Although research in the 1970's tended to assume that availability of demersal resources was limiting to adult populations, studies in the 1980's have demonstrated the importance of recruitment-limitation; larval survival, dispersal, or settlement survivorship may limit adult populations (Sale, 1980; Munro and Williams, 1985; Richards and Lindeman, 1987). Indirect evidence of recruitment limitation includes large spatial and temporal variation in recruitment and adult population size that could not be explained by differences in reef structure (Munro et al., 1973; Sale, 1980; Sale et al., 1984; Munro and Williams, 1985; Shulman, 1985a; Doherty, 1987).

Three lines of direct evidence show the importance of recruitment limitation as opposed to resource limitation in controlling adult population size. First, the lack of density-dependent post-settlement mortality (Doherty, 1982b; Victor, 1983; 1986a) indicates competition or predation may not be as important as larval supply. Second, a shortage of competent larvae can keep reef fish populations below the levels at which the supply of food and space limits population sizes for damselfish (Williams, 1980; Doherty 1982a; 1982b; 1983) and wrasses (Victor, 1983; 1986a; 1986b). Third, greater benthic resources did not increase damselfish abundance (Wellington and Victor, 1985) nor have artificial reefs increased regional reef fish production (Munro and Williams, 1985).

In opposition, Shulman and Ogden (1987) predicted that mortality of post-settlement juveniles would have a much stronger influence on adult population abundance than proportionately equivalent changes in recruitment rate, particularly for species with high natural mortality rates. Recruitment limitation was predicted to be more important for species with low natural mortality. They found that postsettlement mortality had a stronger influence on adult population size than proportionately equivalent changes in recruitment rates for two out of three species for which recruitment limitation had been demonstrated. Also, causes of population limitation can change over time (Wiens, 1977; Ross, 1986). Artificial reefs could increase production of species that are not normally habitat-limited during "environmental crunches" where unusual environmental conditions or extremely good recruitment years increase competition and habitat limitation.

Fishery Exploitation.—Fishery exploitation can be a significant factor in limiting adult population size, especially for long-lived species (Cushing, 1973; Gulland, 1977). Overfishing of tropical reef resources, in particular, has now been documented as a widespread problem (Pauly and Murphy, 1982; Munro, 1983; Appledoorn and Lindeman, 1985; Bohnsack, in press). Surplus production models (Ricker, 1977) predict that the standing stock biomass will be around half of its unexploited value for fisheries operating at the maximum sustained yield (MSY). Biomass should be less for overfished stocks. Samples and Sproul (1985) modeled FAD fisheries and concluded that unregulated, low-cost, efficient fishing effort near fish aggregators could deplete stocks and reduce gross fishery revenues.

Behavioral Studies

Behavioral studies have shown mechanisms applicable to the attraction of reef fishes to artificial reefs. Many fishes tend to orient and position themselves in size-specific and species-specific ways to structure and light (Abel, 1962; Ogawa, 1968; Grove and Sonu, 1985). The most basic mechanisms are instinctive orientation responses (taxes or kinesis) to structure or current and thigmotropic responses (contact with objects) (Breder and Nigrelli, 1938; Ogawa, 1968). Helfman (1979) showed that fishes may move to shade because they can better see objects in surrounding sunlit waters, such as approaching predators or prey. Some fishes may use structure for orientation and navigation purposes without directly obtaining food or shelter (Bohnsack and Sutherland, 1985). Curiosity may be important for some species. Mice have been shown to spend considerable time exploring novel, structurally complex environments that are unlike their home environment (Berlyne, 1966). Structural complexity of artificial reefs may also moderate predation by providing more refuges and thus decrease the foraging efficiency of predators (Menge and Sutherland, 1976; Rosenzweig and MacArthur, 1963; Ware, 1972; Hixon and Beets, 1989).

Reef fishes have been shown to select habitats and to change habitat requirements with age (Sale, 1968; 1969; Starck, 1970). Sale (1969) predicted that fishes will accumulate in preferred habitats through a process of appetitive exploration, where fishes in adequate environments will spend little time explorating new environments while fishes in less adequate environments will spend more time exploring new environments. Wecker (1963) showed the accumulations of mice in preferred habitats because individuals moved slower in preferred habitats and speeded up in less preferred habitats.

Predator abundance at artificial reefs has been correlated with prey availability (Ranasinghe, 1981; Kock, 1982; Buckley and Hueckel, 1985). Predators can accumulate in the vicinity of prey by means of "area restricted searching," where predators slow down their normal movements or increase their rate of turning after finding a prey item (Hassell and May, 1974). Thomas (1974) showed that fishes decrease the linear distance traveled after successfully discovering food and increased it after rejecting a food item. This behavior facilitates avoiding the unproductive foraging areas, increasing the chances of discovering productive areas, and remaining in the proximity of discovered food.

Optimal foraging theory (reviewed by Krebs, 1978; Hughes, 1980; Hart, 1986) could also be applied to movements of fishes, especially predators, between reefs. Fishes are predicted to distribute themselves and to move between reefs so as to maximize net energy gain. Fishes should distribute themselves between reefs according to relative reef profitabilities (food intake) (Godin and Keenleyside, 1984). Theories of "marginal value" (Charnov, 1976; Hart, 1986) and "giving up time" (Krebs et al., 1974; Krebs, 1978; MacNair, 1982) predict that predators should leave a reef when the energy yield from food resources is reduced to a certain level. Foragers should spend more time at reefs with abundant food resources than at reefs with low food availability. Model predictions may be modified to account for unequal foraging and learning abilities, risks of predation, presence of conspecifics, unpredictability of available food, and the costs and time to travel between patches (Regelmann, 1984; Milinski, 1984; Hart, 1986; Milinski, 1986).

Artificial Reef Studies

Bohnsack and Sutherland (1985) reviewed artificial reef literature and found numerous, well-documented observations of rapid colonization rates, high fish densities, and high catch rates. With few exceptions (Burchmore et al., 1985), fish densities, biomass, and catch rates were often higher on artificial reefs than on natural reefs (see also Buckley and Hueckel, 1985; Matthews, 1985). Fishes often appeared within hours and average numbers of individuals and species often occurred within days, weeks, or months. Observations of fish feeding on and around artificial reefs were common. Nelson (1985) reported that gray triggerfish grew faster at oil production platforms than in natural habitats.

Some evidence shows fish attraction and possibly behavioral preference for artificial reefs. Tagging studies have demonstrated fish movement from natural reefs to artificial reefs (but not vice versa) in Puerto Rico (Fast and Pagan, 1974) and in California (Matthews, 1985; Solonsky, 1985). Buckley and Hueckel (1985) demonstrated the importance of rockfish and ling cod immigration in replacing fishery losses on artificial reefs in Puget Sound.

Munro and Williams (1985) noted there was little evidence showing that artificial reefs increased the total fish production in a given area, despite the fact that numerous artificial reefs had been constructed in many parts of the world. Japanese artificial reef programs, the most extensive in the world, were usually justified based on popularity and economics by comparing the value of the harvest to the cost of building reefs (Grove and Sonu, 1985; Mottet, 1985; Nakamura, 1985; Sato, 1985). Grove and Sonu (1985) concluded that the evidence for increased artificial reef productivity from before and after surveys was far from conclusive, even though dramatically increased landings had been reported from particular areas. Mottet (1985) also concluded that insufficient biological data were available to judge the effectiveness and practicality of many of the Japanese enhancement efforts. Sakai (1982, cited in Kawasaki, 1984) concluded that no significant economic benefits were attributable to the artificial reefs after comparing the fish production value between the 5-year period before and the 10-year period after artificial reef installation off Hokkaido, Japan. Kawasaki (1984) examined data from the first two years after a 5-year installation program in Yuriage Miyagi Prefecture, Japan, and found uncertain economic benefits because artificial reefs attracted some species but repelled others. Polovina and Sakai (1989) showed that artificial reefs in one region increased the production of octopus but only aggregated four flatfish species.

Discussion

Attraction and production are not mutually exclusive and can be considered opposite extremes along a gradient. While artificial reefs may merely attract and concentrate some fishes, they may promote the production of others. Most fishes probably lie somewhere between the two extremes.

Behavioral studies show many mechanisms to explain fish attraction to artificial reefs. However, demonstrating attracting mechanisms does not refute the possibility of increased production. Fish attraction behavior presumably evolved because of some selective advantage (i.e., faster growth, increased survival, and reproduction). The concern here is that artificial reefs may provide cues beyond the evolutionary experience of fishes and elicit responses that are not necessarily adaptive. An analogous example is the concentration of fishes in warm water plumes from power plants (reviewed by Goodyear et al., 1974). Under natural situations, moving to the warmest water may be adaptive, but in power plant plumes fishes may spawn at the wrong time of year or die when the plant is temporarily shut down. Similarly, fishes attracted to artificial reefs may face higher mortality from natural predators (Hixon and Beets, 1989) or fishermen (Matthews, 1985; Solonsky, 1985).

Evidence for the five proposed mechanisms for increasing total biomass production with the addition of artificial reefs is limited and mostly circumstantial:

Artificial Reefs Provide Additional Food.—Many studies have reported observations of fishes feeding at artificial reefs. Added substrate undoubtedly provides additional food but it remains to be shown how much new fish biomass is consequently produced and whether the added biomass is a significant contribution to stock size.

Artificial Reefs Increase Feeding Efficiency.—Improved feeding efficiency implies faster growth rates on artificial reefs than for fishes in natural habitat. This has not been demonstrated on a general basis but has been claimed for one species (Nelson, 1985).

Artificial Reefs Provide Shelter from Predation.—Many studies have reported observations of larvae and juvenile fishes at artificial reefs. This is not sufficient evidence because individuals present do not necessarily survive or make a significant contribution to the population. Shelter from predation implies higher survival at artificial reefs than in natural habitats, which was supported by some experimental studies discussed earlier. The significance of increased survival on total stock sizes remains to be determined.

Artificial Reefs Provide Recruitment Habitat for Settling Individuals that Would Have Been Lost to the Biota Otherwise.—This is difficult to test although Polovina and Sakai (1989) provide some supporting evidence for octopus. To my knowledge no other published data support this possibility.

Artificial Reefs Increase the Production of Natural Reef Environments by Creating Vacated Space.—This mechanism is most applicable to unexploited, habitat-limited populations near their environmental carrying capacity; it is less likely to apply to recruitment-limited, heavily fished or overfished populations. Under these conditions, populations are below carrying capacity, face reduced competition, and are less likely to be habitat-limited. However, artificial reefs may help mitigate natural reef damage or loss due to pollution or other causes.

Some of the proposed mechanisms conflict. For example, increased shelter and survival implies reduced predation. However, additional food and increased predator feeding efficiency suggests higher predation rates and increased prey mortality. Also, benefits from changes in one factor may be counteracted by other factors. For example, increased recruitment can be negated by increased mortality from higher fishing intensity on artificial reefs than on natural reefs (Bohnsack and Sutherland, 1985; Matthews, 1985; Solonsky, 1985).

Experimental Approaches

The best direct evidence proving increased production would be an increased total regional catch or standing stock in proportion to the amount of artificial reef material deposited, while controlling for fishing effort, attraction from surrounding areas, and changes in year class strength. While seemingly difficult, one study discussed earlier (Polovina and Sakai, 1989) has met these criteria and has distinguished between mere attraction and new biomass production.

High fish densities, rapid colonization rates, and high catch rates at artificial reefs are well-documented but are not sufficient evidence to prove increased production or habitat limitation. The attraction hypothesis has fewer assumptions, can explain the same phenomena, and should be refuted before increased production is assumed. Both hypotheses, for example, predict high fish densities at artificial reefs. Claiming that habitat is limiting because of high fish densities (or rapid colonization) is analogous to claiming that warm water is limiting because fishes are attracted to warm water plumes from power plants.

Rapid initial colonization likewise can support either hypothesis, except that large fishes aggregating around artificial reefs within days, weeks, or even a few months is clearly the result of attraction. Initial attraction does not refute, however, the possibility of increased production over longer periods. A delayed response would be expected for fish to recruit and grow (Grove and Sonu, 1985).

Both hypotheses can also explain higher catch rates at artificial reefs. However, excessively high catch rates relative to the standing stock size show attraction is operating (Buckley and Hueckel, 1985). Long-term increased Japanese fish landings after installing artificial reefs has been claimed as evidence for increased production, although this information is not conclusive. With the exception of Polovina and Sakai (1989), results do not show whether increased landings were the result of increased fishing effort (or effectiveness), changes in year class strength, or attraction from other areas. Catches in one region may be at the expense of another region. Also unanswered is whether the increased catches could have been made without building artificial reefs.

Determining the importance of attraction and production will require very careful monitoring and assessment of artificial reefs with careful attention to catch rates, fishing effort, species composition, standing stock abundance, recruitment, age composition, growth, and turnover rates. Detailed information about the biology and natural history of resident species would be helpful.

Some indirect evidence supporting increased production by artificial reefs would be provided by experimentally demonstrating the existence of the hypothesized production mechanisms discussed earlier, such as increased growth rate or better survival at artificial reefs. Documenting food web relationships and energy budgets could demonstrate the potential of increased production, especially for food limited systems. Polovina (1984) provided a possible model which estimates mean annual biomass, production, and consumption for ecosystem components. The importance of attraction could be shown by tagging studies, high fishery removal rates relative to standing stock size, and rapid colonization by larger fishes.

Predicted Important Gradients

Based on reviewed literature, I predict several gradients should be important for artificial reef attraction or increased production. These gradients are: natural reef availability, mechanisms of natural population limitation, exploitation pressure, life history dependency on reefs, and species-specific and age-specific behavioral characteristics (Fig. 2). Increased production is most likely at locations isolated from natural reefs; and for habitat-limited, demersal, philopatric, territorial, and obligatory reef species. Attraction should be more important in locations with abundant natural reef habitat; where exploitation rates are high; and for recruitment-limited, pelagic, highly mobile, partially reef-dependent, and opportunistic reef species. Each gradient is discussed below.

Reef Availability.—Munro and Williams (1985) asked whether recruits to artificial reefs would have survived in available natural habitat. I predict artificial reef production should be more important for reef dependent species in locations more isolated from reef habitats. Here potential larval recruits would undoubtedly die if no reef habitat was within range. The proportion of recruits finding suitable habitat should increase with greater habitat availability. Also, species that feed away from reefs are more likely to find unexploited foraging areas in locations isolated from other reefs. Increased production by opening up new foraging areas should be less important with high reef density because surrounding areas are more likely to be exploited by residents of other reefs.

Predictions from behavioral models suggest that fish attraction should be favored at locations with high natural reef availability. Fishes are more likely to select and move between reefs because of reduced travel costs and predation risks with shorter inter-reef distances. Alevizon et al. (1985), Matthews (1985), and Solonsky (1985) provided some support for this model by showing high movement rates to artificial reefs when distances to natural reefs are short.

Population Limitation.—Increased production should be more important for habitat-limited than recruitment-limited species. Both limitations have been demonstrated, although little agreement exists about the species and conditions under which these two factors operate. The ecological literature shows that evidence supporting reef fish habitat-limitation is not as strong as once thought and its acceptance not as widespread as in the past. Even where habitat is limiting, the amount of added artificial reef material may not be significant to population size or economically justified. Huntsman (1981) concluded that although artificial reefs were useful for increasing recreational opportunities, they were impractical for increasing commercial catches because reefs were expensive and time consuming to build and could only provide a small amount of additional habitat relative to available natural habitat. He noted that only four acres of artificial reefs had been constructed in South Carolina after several years of effort. This addition was insignificant relative to the existing natural reef habitat. Ambrose and Swarbrick (1989) suggest similar results for California.

Fishery Exploitation.—Fishery exploitation is likely to significantly affect habitat limitation and production by artificial reefs. Populations exploited at MSY, with approximately half the virgin standing stock biomass of an unexploited stock, should have greatly reduced competition and resource limitation. Overfished

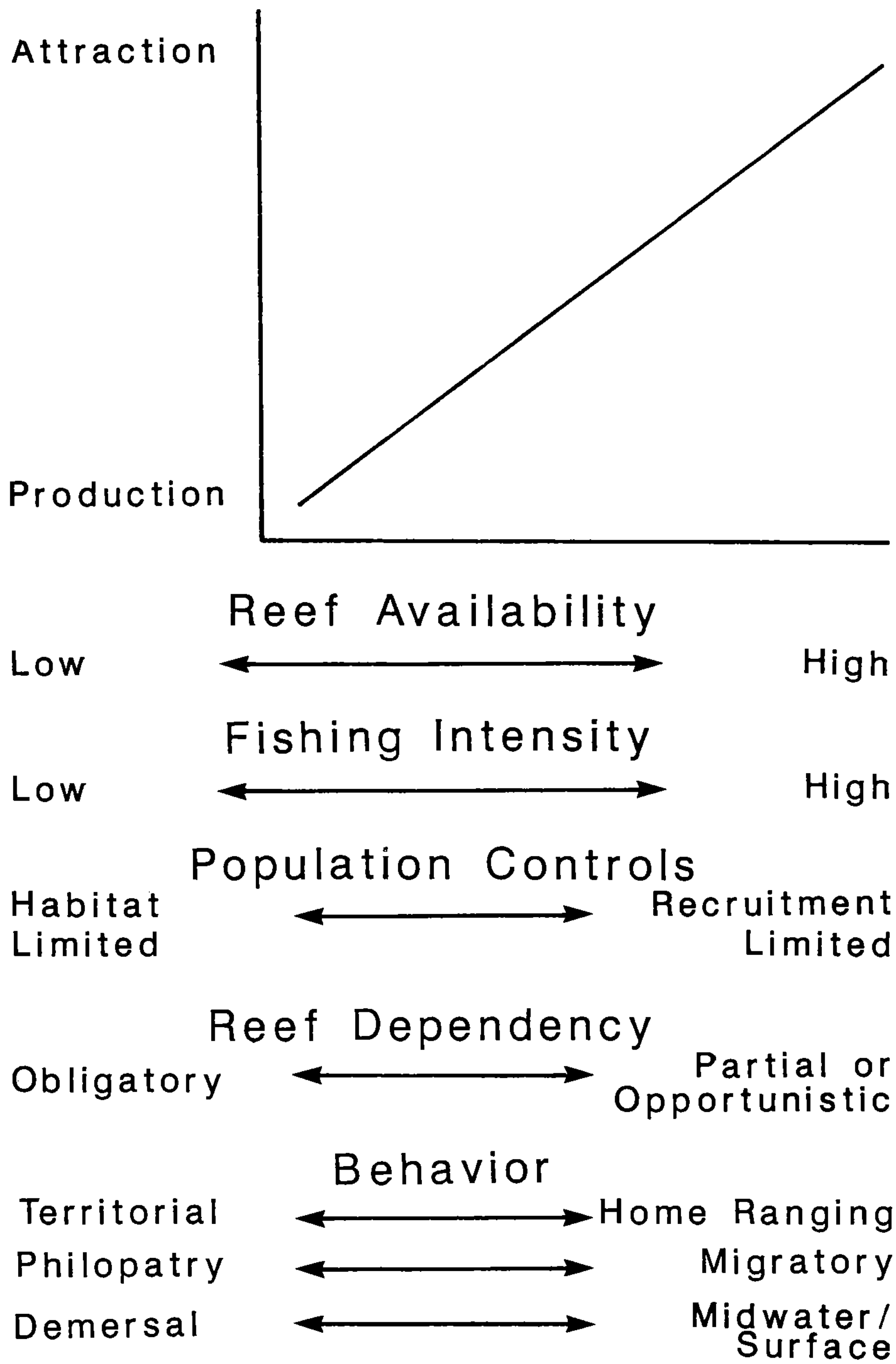

Figure 2. Gradients predicted to be important for attraction or production of fishes at artificial reefs. Linear responses are shown only for illustration purposes.

populations should have even less competition and resource limitation. By definition, recruitment overfishing implies recruitment limitation. Thus, when overfishing occurs, artificial reefs are less likely to increase production. On the other hand, there is no evidence that exploited populations will necessarily be more attracted to artificial reefs.

Life History and Behavior. —Ontogenetic changes and life history have been shown to be important factors. Reef dependency and site attachment varies between species and with age (size) for some species (Sale, 1969). Artificial reefs are unlikely to increase abundance or biomass if bottlenecks to population growth occur in non-reef habitats, or during life history stages not dependent on reefs. For example, reefs designed primarily for adult fishes may not increase production for species that recruit to other habitats, such as many commercially and recreationally important species (e.g., snapper, grouper, grunt, barracuda) that first settle in sand, sea grasses, mangroves, and estuaries. However, suitable enhancement of those habitats may be beneficial.

Production enhancement is more likely for highly territorial, philopatric, and obligatory reef species (e.g., damselfish) that are most likely to be habitat-limited. Attraction should be more important for gregarious, roaming, or facultative reef species (e.g., jacks, barracuda) with less substrate attachment and site dependency because these species are more able to select habitats. Similarly, production enhancement should be more important for demersal species, which are ecologically more closely tied to the benthos, than for surface and midwater pelagic species.

Tests of Predictions. —Polovina and Sakai (1989) provided an independent, partial test for some predicted gradients. Increased production was demonstrated for *Octopus dofleini*, an obligatory demersal reef species that is territorial, philopatric, and has low mobility (Hartwick et al., 1978). In contrast, artificial reefs primarily attracted flatfishes which are more mobile, less territorial, facultative reef species with low philopatry. The octopus appeared also to be habitat-limited while the flatfishes showed some evidence of recruitment-limitation with temporal year class variations independent of habitat availability.

Management Implications

Understanding the extent to which artificial reefs attract or increase fish biomass is important for wise fishery management and the effective construction and deployment of artificial reefs. The relative importance of these two possibilities has not been determined for most species and locations. However, even if artificial reefs primarily redistribute existing fishes, they can still be useful fishery management tools for increasing catchability, making fishes easier to locate, retaining highly migratory species in the local area, and moving stocks closer to fishing ports. Attraction is no problem where (a) fishing effort is low, (b) a large stock reservoir exists relative to catch, (c) fish density is too low to be efficiently fished without artificial reefs, (d) high rates of stock immigration exist, or (e) little natural reef habitat exists. However, while a few reefs can concentrate a stock, too many reefs could again dilute the stock or may not be economically justified.

Artificial reefs may not be effective for increasing fish biomass under some circumstances and enthusiasm for them may detract from more productive management approaches. Artificial reefs may not increase production of recruitment limited populations. If artificial reefs primarily attract fishes, they may not increase total biomass and can even accelerate stock depletion by increasing catchability, especially under heavy fishing pressure. Artificial reefs are unlikely to increase biomass for intensely exploited or overfished populations without other management actions. Interestingly, the incentive to build artificial reefs is most likely to increase when signs of overfishing occur. Under these circumstances other management actions may be needed in addition to, or instead of, building artificial reefs.

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